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GRAZING: WITH PARTICULAR REFERENCE TO BIRCH, JUNIPER AND SCOTS PINE IN THE SCOTTISH HIGHLANDS*

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Summary

This paper briefly reviews the effects of grazing animals in woodlands, with particular reference to birch, juniper and Scots pine in the Scottish Highlands. It emphasises the positive role of large grazing animals in promoting regeneration by creating niches for seedling establishment, as well as discussing the more well known deleterious effects, from the point of view of the forester, of grazing, browsing, bark stripping and trampling, and of attack by insects.

Introduction

Grazing animals are an integral factor in woodland ecology. Through the effects of grazing, browsing, bark stripping and trampling, herbivores are important determinants of tree and shrub establishment and development, and hence of the species composition of woodlands. In the Highlands, red deer (*Cervus elaphus* L.), roe deer (*Capreolus capreolus* L.), brown hare (*Lepus capensis* L.), mountain hare (*L. timidus* L.), rabbits (*Oryctolagus cuniculus* L.), and domestic cattle and sheep occur widely. Other species, *e.g.* Sika deer (*Cervus nippon* Temminck), can be important locally. Woodmice (*Apodemus sylvaticus* L.), voles (*Microtus agrestis* L. and *Clethrionomys glareolus* Schreber) and red and grey squirrels (*Sciurus vulgaris* L. and *S. carolinensis* Gm.) also variously eat seed and damage seedlings, saplings and trees. Many species of insect eat tree seeds and also influence tree growth through defoliation.

Traditionally, most authors have stressed only the destructive role of grazing animals, *i.e.* damage to trees and soil and the prevention of regeneration (Toumey and Korstian, 1937; Spurr and Barnes, 1973). Their more positive role in promoting regeneration through the creation of niches for seedling establishment (Chapman, 1950; Dunlop, 1975; Miles and Kinnaird, 1979) has usually been overlooked or ignored. This is perhaps not surprising, as Nicholson (1974) and Welch (1974) have pointed out that the positive role of grazing animals on British hill land in general has also been widely overlooked or misunderstood.

This paper broadly reviews the effects of grazing animals in woodlands, with particular reference to birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.), juniper (*Juniperus communis* L.), and Scots pine (*Pinus sylvestris* L.), in the Scottish Highlands. It is not comprehensive, and references are quoted mainly as an introduction to the scientific literature.

Grazing and Trampling

In order to establish, any seed requires a suitable niche, or spot permitting germination and seedling survival. This is discussed in more detail

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by Miles and Kinnaird (1979). Large herbivores create niches for germinating seed by trampling, close cropping and occasional tearing up of vegetation, which maintain short swards, shallow moss and litter layers, and expose soil surfaces. For example, Miles (1973) found seedlings of *Betula* spp. and *Pinus sylvestris* growing on patches of ground in Glen Feshie that had been bared by red deer trampling, and has since seen these species growing on spots trampled by sheep, cattle and red deer at many other locations. Apart from fire and windthrow, grazing animals are probably the most important natural agency for creating conditions suitable for tree regeneration. However, while fire and windthrow usually create a much greater density of niches than does grazing, these events occur on average only every 100 years or so at any given site, whereas grazing animals create new niches continuously.

Once young seedlings are present, their continued survival and growth above the field layer canopy, particularly when the latter is an herbaceous sward, may depend on grazing animals. Thus Hallin (1957) found that grazing benefited regeneration of *Pinus jeffreyi* Balf. and *P. ponderosa* Laws. which cannot survive severe competition from vegetation when young. Grazing keeps the field layer shorter and reduces the depth of moss and litter layers. In a *Betula pubescens* wood in Glen Feshie, Kinnaird (unpublished) found that the mean moss and litter depth of 2 cm increased to 8 cm, and varied up to 16 cm in places, four years after fencing out large herbivores. Seedling growth is minimal at the low light intensities found below such deep moss and litter layers, particularly those under woodland, heather (*Calluna vulgaris* (L.) Hull.) and bracken (*Pteridium aquilinum* (L.) Kuhn) canopies. Kinnaird (unpublished) found very poor growth of *Betula pendula* and *B. pubescens* seedlings grown experimentally at 6% relative light intensity (which is about that found under a fairly dense birchwood), and up to 90% mortality from unknown causes. Damping-off can be a major cause of mortality in shade (Taher and Cooke, 1975), particularly for *Betula* spp. (Vaartaja, 1962), and may have been involved in this case.

From a practical viewpoint, this means that fencing off land from large grazing animals usually permits the development only of those grazed-down saplings already present. Few if any new seedlings are likely to establish within at least ten years of fencing because of the accumulation of moss and litter, and the development of a luxuriant field layer. An appreciable number of new seedlings will not appear until dwarf shrub plants or grass tussocks begin to die of old age and form temporary gaps in the sward. Thus, where enclosure is necessary to permit continued sapling growth, only ground with a satisfactory stocking density of existing seedlings and saplings should be fenced.

While much work has been done on the effects of treading by cloven-hoofed animals on pasture vegetation (*e.g.* Thomas, 1960; Edmond, 1970; Frame, 1971), none appears to have been done on the effects on woodland field layers. Because different plant species vary in their reaction to trampling, heavy stocking of pasture swards can produce marked changes in species composition. Similar changes will presumably also occur in

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woodland field layers. Bracken, for example, is more susceptible to mechanical damage than most other species and heavy trampling reduces the abundance and vigour of fronds.

Trampling can damage young saplings. Lull (in Cohron, 1971) estimated that a cattle hoof exerts a pressure of 3·4 kg cm^{-2} compared to 1·3 kg cm^{-2} by sheep and 1·4 kg cm^{-2} by man. Thus, while sheep grazing among established saplings may be acceptable, grazing by cattle may not be. Nakata *et al* (1968) recorded severe trampling damage by cattle in a young plantation of *Betula platyphylla* Sukatchev.

Treading can compact the top layer of soil particles and modify apparent pore density, aeration, water percolation rates and temperature (Frame, 1971). Stoeckeler (1959) showed that treading drastically reduced soil infiltration rates in a *Pinus sylvestris* plantation in Wisconsin from 28 cm $hour^{-1}$ when ungrazed to only 3·1 cm $hour^{-1}$ when grazed, though Steen (1957) found increased infiltration rates after treading at a site in Sweden. Compaction is only severe in soils high in clay or organic matter. Compaction impedes root development (Frame, 1971) and the radicles of germinating seeds may fail to penetrate compacted surfaces. On steep slopes, soil erosion can follow severe treading. Damage to tree roots from poaching by cattle can also sometimes occur (Barr, 1968).

Browsing

Browsing by domestic stock and red deer has, together with fire, largely prevented the regeneration of the original woodland cover in the Highlands, and is still a major force today. While regeneration is prolific in some areas where relatively few animals are present, for example of *Pinus sylvestris* at Rothiemurchus in the western Cairngorms, of *Pinus sylvestris* and *Betula pendula* on the Muir of Dinnet on Deeside, and of *B. pendula* on the hills above Spinningdale in Sutherland, more usually it is sparse or absent. Indeed, Chard (1953) estimated that over 20,000 ha of birch woodland was lost in the Highlands in the first half of this century through suppression of regeneration.

Saplings become increasingly susceptible to browsing as they emerge from the field layer (Miller and Cummins, 1974). Thus over a four year period in an area of high red deer use in Glen Feshie, Kinnaird (unpublished) found an average of 31% mortality of unprotected saplings of *Betula* spp., *Juniperus communis* L., *Pinus sylvestris* and *Sorbus aucuparia* L., compared with only 4% in plots from which deer were excluded. In general, the taller the field layer, the longer will saplings remain relatively unbrowsed and survive. Thus Kinnaird (1974) found that young *Betula* plants had survived for up to 31 years in heather swards, but up to only 10 years in grass swards, which were shorter. Individual trees, especially of *S. aucuparia*, often establish within dense bushes of *J. communis* or *Ulex europaeus* L. where they are protected from browsing, and eventually the saplings grow up through the top of the bushes. Saplings of many species can repeatedly sprout again after being pruned back by browsing, especially broadleaved species. In this way browsed down plants can

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attain quite surprising ages while still retaining the superficial appearance of seedlings. Thus Kinnaird (1974) has found seedling-like saplings of *Betula* spp. aged up to 31 years, while Shaw (1974) found those of *Quercus petraea* (Mattuschka) Liebl. over 25 years old, and Brenneman (1956) those of American *Quercus* spp. up to 37 years old.

Studies of browsing by red deer have shown different orders of preference for tree and shrub species in different places (Dzieciolowski, 1969; Badenoch, 1971). The type and quantities of browse and grazing available influence the selection of species, and seasonal variation in selection occurs. Miller (1971) showed that in Glen Feshie small saplings of *Betula* spp. were browsed apparently at random during the winter, but that at bud burst in May there was active selection by red deer for *Betula*, which continued to September. In contrast, both young saplings and mature bushes of *J. communis* were avoided in summer and mainly browsed from December to March, particularly during periods of snow lie.

The factors controlling selection of material in grazing and browsing are complex. While studies have been made of selection, and a practical understanding of a particular site has been achieved (Dzieciolowski, 1969), the underlying principles are still unknown. Equally, little is known about the animal densities which permit woodland regeneration. Holloway (1967) estimated that a winter density of red deer of less than one deer per 25 ha was needed for regeneration of *Betula* spp., *Larix decidua* Mill. and *P. sylvestris* in Glen Dye, Kincardineshire. In the English New Forest, Peterken and Tubbs (1965) estimated that less than one cow per 1-2 ha, one deer per 3-4 ha, or one pony per 5-7 ha, would permit forest regeneration, though these stocking rates seem surprisingly high. In the United States, Pearson *et al* (1971) found stocking rates in a young *P. elliottii* Engel. plantation of one cow per 8-10 ha had no effect on tree survival. Stocking at one cow per 5 ha killed an appreciable number of plants however, although enough remained to develop a forest canopy. In contrast, a stocking rate of one cow per 20 ha in a *P. palustris* Mill. stand had killed 23% of the plants and reduced the growth of the survivors after five years (Boyer, 1967). Clearly, there is no generally "safe" stocking rate. The point at which appreciable or unacceptable damage occurs will inevitably vary greatly from place to place depending, inter alia, on the animals concerned, on the tree species present and how well they are growing, and on the other forage available.

Grazing by rodents may locally have an appreciable effect. Large numbers of voles (*Microtus agrestis*) have been reported following enclosure of ground for afforestation, the exclusion of large herbivores allowing a build up of suitable cover and food. These plagues are usually short-lived, though some damage to trees can be expected before vole numbers decline. *P. sylvestris* saplings up to 3 m tall have been killed by basal debarking by voles, while Kinnaird (unpublished) has found *Betula pubescens* saplings up to 25 cm tall gnawed through at the base by voles. However, rodents do not normally appear to be a major problem following ground enclosure except as predators of seed and seedlings.

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Bark Stripping

Bark stripping by red deer, cattle, horses and squirrels is common, and has been reported on *Betula* spp., *Pinus sylvestris*, *Salix* spp. and *Sorbus aucuparia* (Ueckermann, 1956, 1960; Anon, 1960; Southern, 1964; Stubbe, 1970) among a wide range of other tree and shrub species. Miles (unpublished) has found basal bark stripping of *Juniperus communis*, which was probably caused by rabbits and hares. The relative palatability of bark of different species has been studied (Szederjei, 195 ; Vuckovic, 1974), but the relative susceptibilities reported are dissimilar, though *Fraxinus excelsior* L. and *Ulmus glabra* Huds. appear highly palatable, while *P. sylvestris* is less so but widely taken.

Szederjei (1957) found that most bark strippings damage by red deer was caused in winter and early spring, though Ueckermann (1956) also reported it as occurring during summer when other food was not scarce. Veen (1973) found that debarking of young *P. sylvestris* by red deer coincided with the period when *Calluna vulgaris* was flowering and not grazed.

Many reasons have been suggested for bark stripping: shortage of other food, the need for roughage when on high quality pasture, a need for minerals or vitamins otherwise deficient, and as a consequence of animals experiencing stress. It is not known to what extent these factors may operate singly or in some degree of combination at different sites. However, being aware of the possible causes, some steps may be taken to control bark stripping when it occurs.

When not severe, bark stripping of mature trees may be of little immediate importance, although the wounds might permit the entry of fungal pathogens which could shorten the life of a tree, particularly of *Betula* spp. However, Kinnaird and Welch (unpublished) found that following severe bark stripping in a stand of *S. aucuparia* about 35% of the affected stems died, the structure and composition of the wood changed, and its shelter value was much reduced. Death of *J. communis* shrubs and *P. sylvestris* saplings, and probably of *Betula* and other species also, can occur locally from debarking by red deer rubbing the velvet off new antlers, and by fraying by roe deer.

Browsing and bark stripping by red deer have been reviewed in more detail by Ueckermann (1960) and Mitchell *et al* (1977).

Effects of invertebrate grazers

By eating forest litter, invertebrates play an important part in its decomposition, and hence have an equally important influence on nutrient cycling and so ultimately on the productivity of the forest itself. However, while many invertebrates, particularly insects, graze on living plant tissues, their effects in natural and semi-natural woods in the Highlands have generally seemed unimportant beside those of vertebrate herbivores. There is no evidence for catastrophic mortality of trees like that caused, for example, by spruce budworm (*Choristoneura fumifera* Clem) on *Abies balsamea* (L.) Mill. in eastern North America (Morris, 1963; Kulman, 1971), by the moth *Operinia autumnata* Bkh. on *Betula pubescens*

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var. *tortuosa* in Lapland (Kallio and Lehtonen, 1975), or more topically by pine beauty moth (*Panolis flammea* Denis & Schiffermüller) on *Pinus contorta* Dougl. in Caithness (Stoakley, 1977).

Defoliating insects can influence regeneration. Thus Shaw (1974) has shown that saplings of *Quercus petraea* can be killed by defoliating caterpillars when low light intensity and/or nutrient stress was already severely limiting growth. The effects of invertebrates on the reproductive cycle of trees have been relatively little studied however. Seed is frequently parasitised on the plant (Miles and Kinnaird, 1979) and preyed upon after dispersal. For example, Vaartaja (1950) noted that *Pinus sylvestris* seeds in central Finland were destroyed by *Lasius* ants, though he also noted that birds ate a far greater quantity of seed. Large numbers of seedlings regularly disappear from unknown causes (Miles 1972, 1973), and grazing by invertebrates probably accounts for much of this mortality. Miles (unpublished) has found that many seedlings of *Juniperus communis* and *P. sylvestris* from experimental sowings at 11 sites in the Highlands were certainly killed by grazing slugs. Howells (1966) found that 52% of *Picea sitchensis* (Bong.) Carr. seed sown in a *P. sitchensis* plantation in North Wales was damaged overwinter by invertebrates, while both he and Scarratt (1966) found that many seedlings were killed by slugs.

It is possible that the cumulative effects of invertebrate herbivores on tree and shrub reproduction may be far greater than is generally recognised. Cantlon (1969) estimated the total effect of invertebrate herbivores on a population of *Melampyrum lineare* Desr., an annual herb of North American woodlands, by repeatedly treating plots with the persistent organochlorine insecticides aldrin and DDT and the organophosphorus insecticide malathion. He found that after two years, the density in spring of young *M. lineare* plants was three times as large as in untreated control plots. This indicates a dramatic effect by invertebrates on natural populations of this plant. No similar study seems to have been done on any tree species, however.

Controlling the Impact of Animals

The effects of large grazing animals are considerable, both by creating niches for seedling establishment and by limiting competition from the field layer on the one hand, and by browsing young saplings and preventing the successful regeneration of woodland on the other hand. Large grazing animals appear to be an important mechanism in the control of woodlands, including the determination of structure and species composition. Most work in this field, however, has been concerned with the description of damage done and the investigation of possible means of control, and there is little understanding of the principles and mechanisms involved.

Suggestions have been made for the use of diversionary feeding *e.g.* sowing and fertilising patches of grass, and winter feeding, as a means of controlling grazing. Kinnaird (unpublished) has recorded negligible browsing of *Betula pubescens* saplings at Inverpolly National Nature Reserve during a year when weather encouraged vigorous and sustained

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growth of herbaceous vegetation compared to that found in both earlier and later years. This suggests that in most years supplementary winter feeding might reduce browsing damage. Red deer are often fed with artificial foods in winter, and large reductions in damage to trees have been reported (Ueckermann, 1960; Strandgaard, 1967; König, 1970). However, several instances are known of severe browsing by red deer even when feed was given. Kinnaird and Welch (unpublished) and Koller (1966) have recorded bark stripping by cattle fed a supplementary winter diet. Indeed, Koller attributed an increase in spring bark stripping to changes in the nature of the supplementary feed creating a demand for roughage.

Enclosures form the most effective way of controlling large herbivores if their overall numbers cannot be reduced. Fences can give complete or partial control of grazing. All large herbivores can be excluded by appropriate fencing; alternatively selected species only can be given access. Thus red deer may have access while domestic stock, rabbits and hares are excluded. Other variations are possible.

Controlled grazing as a form of forest weeding has been successfully applied in plantations in Britain using ewes (Ellice, 1968; Mackeson-Sandbach, 1970), and by cattle and sheep in many other countries (Adams, 1975). There may be considerable scope for this approach, but not enough is known about the effects of different animal stocking rates in plantations with different tree species and field layers. The method requires careful supervision and the freedom to move animals to and from enclosures, at will. Fences, possibly electric, with readily dropped and re-erected wires, may be more suitable for deer. An area can then be made open to grazing by free range animals rather than have animals enclosed within it. The cost of any damage to trees, and possibly also to soils, needs to be considered in the light of the value of the grazings (*e.g.* a revenue from renting them out) and the concomitant forest weeding, *i.e.* reducing competition and thus enhancing sapling growth, and also reducing the risk of fire from an accumulation of readily inflammable litter.

Many areas of decaying *Betula* woodland already have sufficient browsed-down saplings present for a reduction in the grazing levels to permit them to grow up and regenerate the wood (Kinnaird, 1974). When insufficient saplings are present, the grazing animal can be used to create niches and control the competing field layer until sapling numbers are adequate for regeneration. In the absence of a better understanding of plant-herbivore interactions, observation and simple *ad hoc* studies will be of value in determining the course of action required in any wood.

With grazing by invertebrates, the main danger seems to be of a population of defoliating insects reaching a catastrophically high level. Conventionally, attempts to control such epidemics are made with artificial chemicals. Ecologists traditionally maintained that complex ecosystems were more stable than simple ones, though the truth of this seems to hinge on the definition of stability that is adopted (Miles, 1979). Graham (1959) and Belyea (1923) have indeed recommended diversification of tree species as a means of preventing population outbreaks of forest

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pests. There is now considerable experimental evidence that increasing the diversity of plant species present in vegetation can increase the numbers of predators of herbivorous insects (Dempster, 1969; Smith, 1969; Dempster and Coaker, 1973), and also decrease the chances of an invertebrate herbivore finding a suitable host plant (Tahvanainen and Root, 1972; Root, 1973; Feeny, 1976). Root (1973) also suggested that a specialised herbivore may be able to attain a much greater relative density where one host species predominates in vegetation than is possible in a diverse environment. Nevertheless, however sound the ecological arguments for growing trees in mixed species stands rather than monocultures (and the relative effects of pure versus mixed stands on soil properties and on nutrient cycling might also be invoked here), it is apparently not a practical proposition at the moment. However, Feeny (1976) has suggested a possible escape from this dilemma. Plants, especially trees, tend to possess a considerable armoury of chemical defences against attack by herbivores (Freeland and Jantzen, 1974; Levin, 1976). The high degree of host specificity shown by so many phytophagous insects seems to be accounted for by a particular species having co-evolved with its host, and therefore having adapted to a particular toxin or array of toxins. Feeny has suggested that a situation similar to that obtaining where a diversity of plant species exists might be achieved by interplanting different genotypes of the same species, each with a different line of chemical resistance, thus imitating natural interspecific diversity.

References

Adams, S. N. (1975): Sheep and cattle grazing in forests: a review. *J. appl. Ecol.*, **12**, 143-152.

Anon. (1960): The grey squirrel: a woodland pest. *Leafl. For. Commn, Lond.*, **31**.

Badenoch, C. O. (1971): Survey of damage by deer in plantation woodland. *Range Ecology Research, 1st Progress Report*, pp. 45-46. Nature Conservancy, Edinburgh.

Barr, H. (1968): Grazing cattle in trees. *N.Z. Farmer*, 36-38.

Belyea, H. C. (1923): The control of white-pine weevil (*Pissodes strobi*) by mixed planting. *J. For.*, **21**, 384-390.

Boyer, W. D. (1967): Grazing hampers development of longleaf pine (*Pinus palustris*) seedlings in southwestern Alabama. *J. For.*, **65**, 336-338.

Brenneman, W. S. (1956): Age of oak "seedlings." *J. For.*, **54**, 774-775.

Cantlon, J. E. (1969): The stability of natural populations and their sensitivity to technology. *Brookhaven Symp. Biol.*, **22**, 197-205.

Chapman, H. H. (1950): *Forest Management.* The Hildreth Press, Boston, Conn.

Chard, J. S. R. (1953): Highland birch. *Scott. For.*, **7**, 125-128.

Cohron, G. T. (1971): Forces causing soil compaction. *Compaction of Agricultural Soils*, pp. 106-122. American Society of Agricultural Engineers, Michigan.

Dempster, J. P. (1969): Some effect of weed control on the numbers of the small cabbage white (*Pieris rapae* L.) on Brussels sprouts. *J. appl. Ecol.*, **6**, 339-345.

Dempster, J. P. and Coaker, T. H. (1973): Diversification of crop ecosystems as a means of controlling pests. *Biology in Pest and Disease Control.* (Ed. by D. Price Jones and M. E. Solomon), pp. 106-114. Blackwell Scientific Publications, Oxford.

Dunlop, B. M. S. (1975): The regeneration of our native pinewoods. *Scott. For.*, **29**, 111-119.

SCOTTISH FORESTRY ©

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Dzieciolowski, R. (1969): *The Quantity, Quality and Seasonal Variation of Food Resources Available to Red Deer in Various Environmental Conditions of Forest Management.* Forest Research Institute, Warsaw.

Edmond, D. B. (1970): Effects of treading on pastures, using different animals and soils. *Proc. 11th Int. Grassld Congr.*, 604-608.

Ellice, A. M. (1968): Sheep may safely graze. *Scott. For.*, **22**, 320-322.

Feeny, P. (1976): Plant apparency and chemical defense. *Recent Adv. Phytochem.*, **10**, 1-40.

Frame, J. (1971): Fundamentals of grassland management. Part 10. The grazing animal. *Scott. Agric.*, **50**, 28-44.

Freeland, W. J. and Janzen, D. H. (1974): Strategies in herbivory by mammals: the role of plant secondary compounds. *Am. Nat.*, **108**, 269-289.

Graham, S. A. (1959): Control of insects through silvicultural practices. *J. For.*, **57**, 3-32.

Hallin, W. E. (1957): Silvicultural characteristics of Jeffrey pine. *Cal. For. Range Exp. Sta. Tech. Pap.*, No. 11.

Holloway, G. W. (1967): *The effect of red deer and other animals on naturally regenerated Scots pine.* Ph.D. Thesis (unpublished), University of Aberdeen.

Howells, G. (1966): *Some factors affecting development of natural regeneration of Sitka spruce.* Ph.D. Thesis (unpublished), University of Wales.

Kallio, P. and Lehtonen, J. (1975): On the ecocatastrophe of birch forests caused by *Oporinia autumnata* (Bhk.) and the problem of reforestation. *Fennoscandian Tundra Ecosystems. Part 2. Animals and systems Analysis* (Ed. by F. E. Wielgolaski), pp. 174-180. Springer, Berlin.

Kinnaird, J. W. (1974): Effect of site conditions on the regeneration of birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.). *J. Ecol.*, **62**, 467-472.

Koller, O. (1966): Schälschaden durch Wiedevieh. *St. Hubertus*, **3**, 3.

König, E. (1970): Effects of fresh food on the prevention of peeling damage by red deer. *Proc. Int. Congr. Game Biol.*, **9**, 176-181.

Kulman, H. M. (1971): Effects of insect defoliation on growth and mortality of trees. *Ann. Rev. Ent.*, **16**, 289-324.

Levin, D. A. (1976): The chemical defenses of plants to pathogens and herbivores. *Ann. Rev. Ecol. Syst.*, 7, 121-159.

Mackeson-Sandbach, G. L. (1970): Weeding plantations with sheep. *Timb. Grower, Kenilworth*, **35**, 35.

Miles, J. (1972): Experimental establishment of seedlings on a southern English heath. *J. Ecol.*, **60**, 225-34.

Miles, J. (1973): Early mortality and survival of self-sown seedlings in Glenfeshie, Inverness-shire. *J. Ecol.*, **61**, 93-98.

Miles, J. (1979): *Vegetation Dynamics.* Chapman & Hall, London. (In press).

Miles, J. and Kinnaird, J. W. (1979): The establishment and regeneration of birch, juniper and Scots pine in the Scottish Highlands. *Scott. For.*, **33**.

Miller, G. R. (1971): Grazing and the regeneration of shrubs and trees. *Range Ecology Research, 1st Progress Report*, pp. 27-40. Nature Conservancy, Edinburgh.

Miller, G. R. and Cummins, R. P. (1974): Liability of saplings to grazing on red deer range. *Institute of Terrestrial Ecology, Research in Scotland, Report for 1971-73*, pp. 31-33. Institute of Terrestrial Ecology, Banchory.

Mitchell, B., Staines, B. W. and Welch, D. (1977): *Ecology of Red Deer. A research review relevant to their management in Scotland.* Institute of Terrestrial Ecology, Cambridge.

Morris, R. F. (Ed.), (1963): The dynamics of epidemic spruce budworm populations. *Mem. ent. Soc. Can.*, No. 31.

Nakata, I., Yokoyama, C., Mori, K. and Shibata, Y. (1968): Cattle grazing in a new plantation of broadleaved trees. *Ann. Rep. For. Exp. Sta., Hokkaido*, 1967, 61-73.

Nicholson, I. A. (1974): Red deer range and problems of carrying capacity in the Scottish Highlands. *Mammal Rev.*, **4**, 103-118.

SCOTTISH FORESTRY ©

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Pearson, H. A., Whitaker, L. B. and Duvall, V. L. (1971): Slash pine regeneration under repeated grazing. *J. For.*, **69**, 745-746.

Peterken, G. F. and Tubbs, C. R. (1965): Regeneration in the New Forest, Hampshire, since 1650. *J. appl. Ecol.*, **2**, 159-170.

Root, R. B. (1973): Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol. Monogr.*, **43**, 95-124.

Scarratt, J. B. (1966): *Investigations into the germination, early growth and survival of Sitka spruce seedlings under natural and artificial conditions.* Ph.D. Thesis (unpublished), University of Wales.

Shaw, M. W. (1974): The reproductive characteristics of oak. *The British Oak. Its History and Natural History* (Ed. by M. G. Morris and F. H. Perring), pp. 162-181. E. W. Classey, Farringdon.

Smith, J. G. (1969): Some effects of crop background on population of aphids and their natural enemies on Brussels sprouts. *Ann. appl. Biol.*, **63**, 326-330.

Southern, H. N. (Ed.) 1964): *The Handbook of British Mammals.* Blackwell, Oxford.

Spurr, S. H. and Barnes, B. V. (1973): *Forest Ecology*, 2nd edn. The Ronald Press, New York.

Steen, E. (1957): The effect of cattle grazing upon plant cover and soil in a freshwater marshy meadow. *Meddn St. JordbrFörs.*, No. 83.

Stoakley, J. T. (1977): A severe outbreak of the Pine Beauty moth on Lodgepole pine in Sutherland. *Scott. For.*, **31**, 113-125.

Stoeckeler, J. H. (1959): Trampling by livestock drastically reduces infiltration rate of soil in oak and pine woods in southwestern Wisconsin. *Lake States For. Exp. Sta. Tech. Note*, No. 556.

Strandgaard, H. (1967): En undersøgelse over kronvildtets tilpasning til det danske kulturlandskab. *Dansk Viltunders.*, **13**, 9-75.

Stubbe, C. (1970): Barking damage by red deer in forestry—causes, effects and prevention. *Wiss. Z. tech. Univ. Dresden*, **19**, 171-178.

Szederjei, A. (1957): Uber das Schälen des Rotwildes. *Z. Jagdwiss.*, **3**, 101-107.

Taher, M. M. and Cooke, R. C. (1975): Shade-induced damping-off in conifer seedlings. I. Effects of reduced light intensity on infection by necrotrophic fungi. *New Phytol.*, **75**, 567-572.

Tahvanainen, J. O. and Root, R. B. (1972): The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia*, **10**, 321-346.

Thomas, A. S. (1960): The tramping animal. *J. Br. Grassld Soc.*, **15**, 89-93.

Toumey, J. W. and Korstian, C. F. (1937): *Foundations of Silviculture upon an Ecological Basis*, 2nd edn. Wiley, New York.

Ueckermann, E. (1956): Untersuchungen über die Ursache des Schälens des Rotwildes. *Z. Jagdwiss.*, **2**, 123-131.

Ueckermann, E. (1960): *Wildstandsbewirtschaftung und Wildschadenverhütung beim Rotwild.* Paul Parey, Berlin.

Vaartaja, O. (1950): On factors affecting the initial development of pine. *Oikos*, **2**, 89-107.

Vaartaja, O. (1962): The relationship of fungi to survival of shaded tree seedlings. *Ecology*, **43**, 547-549.

Veen, H. E. van de (1973): Bark stripping of coniferous trees by red deer. *Deer*, **3**, 15-21.

Vuckovic, M. (1974): Results of introducing red deer (*Cervus elaphus*) in the virgin forest of the National Park "Biogradska Gora." *Trans XIth Int. Contr. Game Biol.*, 565-571.

Welch, D. (1974): The floristic composition of British upland vegetation in relation to grazing. *Land*, **1**, 59-68.

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